

## SYNOPSIS OF *STEPHANODORIA* (ASTERACEAE: ASTEREAEE)

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### ABSTRACT

A full description and citation of specimens are provided for the monotypic Mexican genus *Stephanodoria*. *Stephanodoria tomentella* is restricted to a small area of northeastern San Luis Potosí, where it is rare and in danger of extinction. The species is part of the "*Xanthocephalum* group" of the subtribe *Machaerantherinae*, but its phylogenetic position within the *Xanthocephalum* group is not clearly resolved. Some aspects of possible relationships among other genera of this group also are discussed.

KEY WORDS: *Stephanodoria*, Asteraceae, México, taxonomy

The single species that comprises *Stephanodoria* E. Greene was first described by Robinson (1892) as a species of *Xanthocephalum* Willd. It was formally excluded from the latter by Greene (1895), who created the new genus for it. After that, it was not discussed or included in published studies evaluating relationships among *Astereae* until the recent dissertation by Suh (1989) and its publication by Suh & Simpson (1990), who substantiated Greene's rationale for placing *Stephanodoria* as a monotypic genus closely related to *Xanthocephalum*.

*Stephanodoria tomentella* (B.L. Rob.) Greene is represented in herbaria by only a few specimens, including the type material collected by Pringle and a few much more recent collections from near the type locality. Because *Stephanodoria* is poorly known and endangered in its continued existence, a full description and citation of specimens are provided.

*STEPHANODORIA TOMENTELLA* (B.L. Robinson) E. Greene

*Stephanodoria tomentella* (B.L. Rob.) E. Greene, gen. & comb. nov. *Erythea* 3:12. 1895. BASIONYM: *Xanthocephalum tomentellum* B.L. Rob., Proc. Amer. Acad. Arts 27:172. 1892. TYPE: MEXICO. San Luis Potosí: alkaline

meadows, Hacienda de Angostura [ca. 7 mi SSW of San Bartolo], 11 Jul 1891, C.G. Pringle 3761 (HOLOTYPE: GH; Isotypes: LL!, MU!).

Perennial herbs from woody roots, producing short basal offsets, (0.5-)1.3-2.3 m tall, branching primarily in the inflorescence; stems, leaves, and phyllaries stipitate-glandular and minutely hirtellous-pilosulous, not glutinous. Leaves thick and noticeably fleshy when fresh, the basal ones numerous, persistent, the blades obovate-oblong-elliptic, entire, mostly 15-30 cm long, 12-40 mm wide, basally attenuate to a petiole 3-12 cm long and 1/4-3/5 the length of the leaf; cauline leaves reduced in size, becoming sessile upwards. Heads in an open, loose corymb, sessile to short-pedicellate in corymboid clusters of 2-6; pedicels 0.5-1.0 mm long; involucre turbinate, 4.5-6.0 mm long, 3-5 mm wide; phyllaries strongly graduated in 5-7 series with the outermost 1/4-1/3 as long as the inner, oblanceolate-obovate, mostly indurated, the apex greenish, spreading to reflexed, the lateral margins with a thin, hyaline rim, apical margins often minutely stipitate-glandular; receptacles slightly convex, with low alveolar ridges. Ray flowers ca. 20-30, golden-yellow, pistillate and fertile, with corollas 4.2-5.0 mm long, sparsely and minutely stipitate-glandular on the tube, and ligules 1.2-1.5 mm long, 0.3-0.5 mm wide. Disc flowers fertile, yellow, minutely stipitate-glandular on the tube and lower limb, erect except for the outer, which lean outward after elongation of the tube, with corollas 3.5-4.0 mm long, including the 2.0-2.5 mm long tube, elongating at maturity and elevating the corolla during anthesis, abruptly widened into the limb, with the deltate lobes 0.2-0.4 mm long, erect; anthers inserted ca. halfway down the tube, with the tube usually becoming noticeably different in color and texture at that point; style branches with deltate-triangular collecting appendages. Achenes mostly oblanceolate-oblong to oblong-elliptic, strongly flattened, 2-sided with 2 thick ribs or sometimes with a narrow third side and third rib, 1.3-1.8 mm long, 0.6-0.9 mm wide, straw-colored, shiny, glabrous or very sparsely short-strigose only at the apex; pappus a hyaline, lacerate- or erose-margined corona 0.3-0.5 mm high, or sometimes 1-sided and somewhat awn-like.

Flowering from June to October. Chromosome number,  $2n=6II$  (Lane 2920, reported by Lane & Li 1993; Nesom & Wells 6681, reported here from a count obtained from field-collected buds).

The generic name is derived from the Greek elements "stephanos" ("crown," referring to the coroniform pappus) and "doria" (an early name for the goldenrod *Solidago*).

Additional collections examined: MEXICO. San Luis Potosí: Mpio. Cd. del Maiz: 0.65 km N of the Escuela Primeria in Las Tablas, 27 Jul 1979, Lane 2535 (TEX); Las Tablas, Lane 2920 (COLO, not seen); 1.2-1.6 mi N of Las Tablas (RR crossing in town), 14 Sep 1988, Nesom & J. Wells 6681 - voucher for chromosome count and chloroplast DNA studies (distributed to ARIZ, CAS, F, GH, M, MEXU, MO, NY, PATZ, RM, TEX, US); Mpio. Cerritos, near the railroad station at Cerritos, Jun 1981, Leidig & Lane s.n. (TEX).

*Stephanodoria* is endemic to a small area of northeastern San Luis Potosí near the towns of Cerritos, Las Tablas, and San Bartolo. The elevation ranges from about 950 to 1050 meters (as determined from topographic map). The plants grow in low, periodically wet, grassy pockets in areas of gypseous-alkaline meadows with scattered

mesquite, juniper, and succulent-leaved shrubs and herbs including *Lycium*, *Maytenus*, *Flaveria*, *Samolus*, *Sesuvium*, and *Suaeda*. Pringle described the distinctive area around Las Tablas in his diary (Davis 1936) as "meadows miles in extent, covered with deep grass, interrupted by belts of juniper forest and bounded by gray desert hills of half-bare lime-rock. These meadows appear to rest on a subterranean lake. A tough sod and layer of black soil a few feet in thickness covers mud and water." *Sporobolus airoides* (Torr.) Torr. is one of the dominant grass species.

The gypseous soil in this area is derived from the exposed gypsum and gypseous limestone of the surrounding hills and mountains (the "gray desert hills" described by Pringle). The ancient nature of this habitat is attested to by the occurrence of other gypsophilic endemics restricted to the same immediate area or nearly so: *Oldenlandia pringlei* B.L. Rob., *Pluchea mexicana* (Godfrey) Nesom, *Viguiera potosina* Blake, *Pinaropappus multicaulis* Brandegee, and *Geissolepis suaedifolia* B.L. Rob. Both *Stephanodoria* and *Geissolepis* are monotypic and are strongly divergent in morphology compared to their closest relatives.

The water table around Las Tablas and Angostura (the type locality) apparently has been lowered by artificially channeled drainage and the area is being modified in other ways. Much of it has been brought into pasturage and in 1988 the continued existence of *Stephanodoria* was estimated to be seriously endangered.

The *Stephanodoria* population sampled by Nesom & Wells in 1988 immediately north of Las Tablas consisted of about 50 to 75 individuals scattered along low areas near the road. The population of *Stephanodoria* sampled in 1981 by Lane & Leidig within the town of Cerritos could not be relocated in 1988 by the present author, apparently because the area in the vicinity of the railroad station is almost entirely under cultivation.

#### Phylogenetic position of *Stephanodoria*

In transferring *Xanthocephalum tomentellum* to *Stephanodoria*, Greene (1895, p. 12) noted that it is

"a plant not far removed in nature from *Solidago rigida*, but with a coroniform rather than capillary pappus, [which] on account of a mere analogy of its pappus, has been published under the wrong genus. . . . Typical *Xanthocephalum* has no pappus at all, but a turgid annulus instead; and the genus should be limited to those species, apparently. But neither the habit, the inflorescence, the involucre nor even the compressed achenes of this plant are at agreement with *Xanthocephalum* or any of its near allies."

The habit and overall appearance of *Stephanodoria* are indeed similar to *Oligoneuron (Solidago) rigidum* (L.) Small, as observed by Greene, but these two species are relatively distantly separated within the Astereae (Nesom 1994) and their similarities are convergent. Recent data (below) support Robinson's original

hypothesis that *Stephanodoria* and *Xanthocephalum* are closely related, but Greene's exclusion of *Stephanodoria* from *Xanthocephalum* has not been formally challenged by any subsequent students of the Astereae.

Morphological and molecular evidence that *Stephanodoria* is most closely related to a small cluster of genera, including *Xanthocephalum*, is summarized by Lane, *et al.* (1996). This is the "*Xanthocephalum* group" (Nesom 1994): *Xanthocephalum*, *Stephanodoria*, *Isocoma* Nutt., *Rayjacksonia* Hartman & Lane, *Grindelia* Willd. (including *Prionopsis* Nutt.), and *Olivaea* Benth. (= the "*Grindelia* group" in Figure 9 of Lane, *et al.*). Evidence for membership of the *Xanthocephalum* group within the strongly defined, North American *Machaeranthera* Nees clade was shown in the molecular data of Suh (1989) and Morgan (1990), summarized by Nesom, *et al.* (1990), and corroborated in Lane, *et al.* (1996) in a broader context. The *Xanthocephalum* group was formally placed within the subtribe Machaerantherinae by Nesom (1994).

The large, thick, entire, oblanceolate leaves of *Stephanodoria* are remarkably similar to those in some species of *Pyrrocoma* Hook. (e.g., *P. crocea* [A. Gray] Greene), more so than to any in the *Xanthocephalum* group. *Pyrrocoma* is a member of the Machaerantherinae but consistently placed outside of the *Xanthocephalum* group (Suh 1989; Morgan 1990; Morgan & Simpson 1992). The strongly flattened and elongate achenes of *Stephanodoria* also are more similar to those of *Pyrrocoma* than to any of the *Xanthocephalum* group. Mayes (1976) postulated that a close relationship might exist between *Pyrrocoma* and *Rayjacksonia*, based on their mutual production of flavones. Broader evidence, however, indicates that the similarity between *Pyrrocoma* and *Stephanodoria* (as well as *Rayjacksonia*) has resulted from evolutionary parallelism (but still reflective of close common ancestry).

*Stephanodoria* and *Xanthocephalum* are positioned essentially as sister taxa by molecular data (Lane, *et al.* 1996; Lane & Hartman 1996), but there is little in their morphology leading to the same conclusion. The two are placed as sister taxa in only two of the five trees based solely on morphology (Lane & Hartman 1996, Figures 1-5). Plants of both genera produce a coroniform pappus and sparsely pilose and stipitate-glandular ray and disc corolla tubes. Lane & Hartman scored achenes of both as glabrous, but in my observations both have minute twin-hairs near the fruit apex. The lack or slowness of coiling of the ray corollas also might be taken as a similarity between the two genera. In the DNA-based analyses of Lane & Hartman, the two genera as a pair are placed in various positions relative to others of the *Xanthocephalum* group.

Other taxa of the *Xanthocephalum* group

*Grindelia*, *Prionopsis*, and *Olivaea*

The monotypic *Prionopsis* has been treated as a species of *Grindelia* (Nesom, Suh, & Simpson 1992). The molecular data of Lane, *et al.* (1996) support this positioning, but Lane & Hartman (1996) maintained these two as distinct genera because of two morphological differences (besides the pappus) (p. 368): "In *Prionopsis*, the

phyllaries are abaxially eglandular and the leaf apices and marginal teeth are each tipped by a long, soft bristle, while in *Grindelia* the phyllaries are punctate-glandular, and equivalent bristles are missing from the leaves." At least some Mexican species of *Grindelia*, however, have distinctly indurate-spinulose teeth (Nesom 1990) surely homologous with the spinulose teeth of *Prionopsis*, which are drawn out to greater length. I have not surveyed the species for the phyllary character, but even if the difference should hold true, it would be weak rationale for maintaining a generic distinction.

Further evidence that *Grindelia* and *Prionopsis* have immediate common ancestry is found in the disc corolla throats (in *Prionopsis* and every *Grindelia* species I have examined), which produce large, elongate, highly distinctive prismatic crystals characteristic of no other species of the *Xanthocephalum* group (Nesom, Suh, & Simpson 1992). This character was not discussed or scored by Lane & Hartman (1966).

Finally, the comment by Lane & Hartman (1996, p. 368) that "*Grindelia* and *Prionopsis* are sister groups in all of the trees that result from analyses that include that molecular data" is incomplete without reference to the molecular studies by Suh (1989) and Lane, *et al.* (1996). Those studies included six species of *Grindelia* s. str. (vs. only one species in Lane & Hartman), and the accompanying analyses in both broader studies show *Prionopsis* phyletically imbedded within *Grindelia* (vs. a sister relationship).

The ditypic Mexican genus *Olivaea* was observed by De Jong & Beaman (1963) to be closely related to *Grindelia* as well as to *Xanthocephalum*, and McVaugh (1984, p. 643) noted that *Olivaea* is separated from *Grindelia* "by no very fundamental characters." The similarity between *Olivaea* and *Grindelia* is seen in their relatively large and conspicuously radiate heads, linear-lanceolate phyllaries, and dimorphic, somewhat blocky, glabrous achenes with caducous pappus elements. *Olivaea* species also have slightly clasping leaves (scored as sessile by Lane & Hartman). They differ from *Grindelia* in their aquatic habitat, hollow stems, leaves without resinous punctations, united phyllary bases that are chartaceous rather than indurate, winged achenes, pappus of antrorsely barbellate bristles, and lack of prismatic crystals in the disc corolla throats. Except for the pappus, these features could have resulted through simple modifications of *Grindelia* morphology (as implied, I believe, by McVaugh's comment). No molecular data have been available for *Olivaea*, but the morphological analyses by Lane & Hartman show the genus in a variable position within the *Xanthocephalum* group.

Even in view of a weak morphological hypothesis of sister relationship between *Grindelia* and *Olivaea*, the rest of the *Xanthocephalum* group (*Rayjacksonia*, *Isocoma*, *Stephanodoria*, *Xanthocephalum*) is decidedly heterogeneous. Plants of these four genera all produce non-clasping leaves, and the latter three have small heads and ray flowers small or consistently absent. The comment by Lane & Hartman (1996, p. 367) that it "seems likely that these [genera] did not arise in strictly dichotomous fashion" is substantiated by the difficulty in finding synapomorphic morphological features not apparently under simple genetic control.

*Rayjacksonia*

Hartman (1976, 1990) originally recognized the three species of the *Haplopappus/Machaeranthera* "phyllocephalus group" as an undescribed genus closely related to *Xanthocephalum*. Description of the new genus and new combinations were provided as *Rayjacksonia* Hartman & Lane (1996). The three species of *Rayjacksonia* are coherent in vestiture, spinulose foliar teeth, solitary heads, and ray flowers with prominent ligules, but they apparently lack a set of morphological features that could be interpreted as specialized. Two species have monomorphic achenes and phyllaries strongly indurate at the base, while *R. phyllocephala* (DC.) Hartman & Lane produces dimorphic achenes (apparently developed in parallel with those of *Grindelia* and *Olivaea*) and completely herbaceous (non-indurate) phyllaries.

*Xanthocephalum humile*

One of the most interesting problems remaining in the *Xanthocephalum* group is the nature of the relationship of *X. humile* Benth. to the rest of the genus and the generic group. Suh's molecular data show this species more closely related to *Isocoma pluriflora* (Torr. & Gray) Greene than to other species of *Xanthocephalum*. Natural hybrids between *X. humile* and *I. veneta* Kunth have been collected from several localities in central México (Hartman & Lane 1991). The analysis by Lane, *et al.* (1996), in contrast, shows *X. humile* basal to a clade that includes the rest of *Xanthocephalum* as well as *Stephanodoria*. Although *X. humile* is set apart from the rest of *Xanthocephalum*, its closest morphological similarity with those species seems apparent. It will be interesting to see if further studies provide evidence for this.

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